

**Insights into chameleons of the genus *Trioceros*  
(Squamata: Chamaeleonidae) in Cameroon,  
with the resurrection of *Chamaeleon serratus* Mertens, 1922**

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**Abstract.** Relationships among chameleons of the genus *Trioceros* in Cameroon are reviewed on a molecular basis using mitochondrial genes and by morphology. *Trioceros oweni* is placed basal to two distinct clades (lowland-submontane species vs. submontane-montane species) and its position is discussed due to high genetic differences to the remaining taxa. Within the lowland-submontane species group, distinct subclades with low genetic differences exist within *T. montium* and *T. cristatus*. Differing relationships to previously published results are observed within the submontane-montane species group, resulting in taxonomic changes: *Trioceros eisentrauti* is grouped with the two *T. quadricornis* subspecies, showing only low genetic differences, which also correlates with the similar overall morphology. The taxon is thus assigned to a subspecific rank: *T. quadricornis eisentrauti*. Within the *wiedersheimi*-group, the former southern subspecies is elevated to species rank, *Trioceros perreti*, and two additional species have been distinguished by molecular and morphological methods in the former nominate taxon. *Trioceros wiedersheimi* is restricted to northernmost localities, while remaining populations have been assigned to the revalidated taxon *Trioceros serratus* (Mertens, 1922). Differentiating morphological characters for the three species are provided and a neotype of *Chamaeleon serratus* Mertens, 1922 is designated and described to ensure clarification of its taxonomic status and type locality.

**Key words.** Reptilia, Chamaeleonidae, *Trioceros*, *Trioceros serratus*, Africa, Cameroon, phylogeny, taxonomy.

## INTRODUCTION

Only recently, Tilbury & Tolley (2009) provided molecular evidence that the two former subgenera (*Chamaeleo* Laurenti, 1768 sensu stricto and *Trioceros* Swainson, 1839) of the chamaeleonid genus *Chamaeleo* as recognized by Klaver & Böhme (1986) represent two distinct and valid genera. For a diagnosis of the two genera see Klaver & Böhme (1986, 1992) and Tilbury & Tolley (2009). Klaver & Böhme (1992) additionally provided a detailed overview of formerly published knowledge on the

*cristatus*-subgroup inside the *Trioceros*-group from Cameroon.

The Republic of Cameroon exhibits a very high diversity of chameleon species compared to adjacent countries, especially in montane areas (Böhme & Klaver 1981; Gonwouo et al. 2006; Herrmann et al. 2005, 2006). At present 14 species of chameleons are known to occur in Cameroon. They belong to the genera *Chamaeleo* [five

species: *C. africanus* Laurenti, 1768; *C. dilepis* Leach, 1819; *C. gracilis* Hallowell, 1842; *C. quilensis* Bocage, 1886; *C. senegalensis* Daudin, 1802], *Rhampholeon* [one species: *R. spectrum* (Buchholz, 1874)] and *Trioceros* [eight species: *T. camerunensis* (Müller, 1909); *T. cristatus* (Stutchbury, 1837); *T. eisentrauti* (Mertens, 1968); *T. montium* (Buchholz, 1874); *T. oweni* (Gray, 1831); *T. pfefferi* (Tornier, 1900); *T. quadricornis* (Tornier, 1899); *T. wiedersheimi* (Nieden, 1910)]. *Trioceros quadricornis* and *T. wiedersheimi* are polytypic, with one more subspecies [*T. q. gracilior* (Böhme & Klaver, 1981), *T. w. perreti* (Klaver & Böhme, 1992)], resp. (Böhme & Klaver 1981; Chirio & LeBreton 2007; Gonwouo et al. 2006; Klaver & Böhme 1986; Tilbury & Tolley 2009). According to Klaver & Böhme (1997) and Uetz & Hallermann (2010) one additional species (*Chamaeleo laevigatus* Gray, 1863) is present in Cameroon, but this species has not been listed by other recent authors (Chirio & LeBreton 2007; Gonwouo et al. 2006; Tilbury 2010). While some species such as *Chamaeleo gracilis* or *Trioceros cristatus* show a large distribution ranging at least from Nigeria to Gabon and the Congo (Nečas 2004), five species are regarded as montane endemics occupying restricted high elevation areas along the Cameroon mountain chain, with *T. eisentrauti* the most restricted, being endemic to the Rumpi Hills in western Cameroon (Chirio & LeBreton 2007; Gonwouo et al. 2006; Klaver & Böhme 1992).

Pook & Wild (1997) published a preliminary phylogeny of *Trioceros* from Cameroon, and we herein provide additional and new insights into this species group based on additional material.

## MATERIAL AND METHODS

In all, 49 combined, mitochondrial 16S and 12S rRNA gene fragments, sequences (Tab. 1, Appendix II; museum acronyms see below) comprising 964 bp (lengths referring to the aligned sequences including gaps) were obtained. One short section (4 bp from the 12S gene) was too variable to be reliably aligned, and was excluded from the analyses, resulting in a total of 960 bp which were used in the analyses. *Kinyongia tavetana* (AM422414/AM422433; Mariaux et al. 2008) was used as outgroup. Its position outside of *Trioceros* was demonstrated by Tilbury & Tolley (2009). DNA was extracted using QiAmp tissue extraction kits (Qiagen) and the peqGold Tissue DNA Mini Kit (PEQLAB Biotechnologie GmbH) (see Wagner et al. 2009a). The primers 16sar-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr-H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of Palumbi et al. (1991) were used to amplify a portion of the mitochondrial 16S ribosomal RNA gene. Additionally, a section of the mitochondrial 12S ri-

bosomal RNA gene was amplified using the primers 12SA-L (light chain; 5' – AAA CTG GGA TTA GAT ACC CCA CTA T – 3') and 12SB-H (heavy chain; 5' – GAG GGT GAC GGG CGG TGT GT – 3') of Kocher et al. (1989). PCR cycling procedures were as described in Schmitz et al. (2005). PCR products were purified using Qiaquick purification kits (Qiagen). Sequences were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (Thompson et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall 1999). PAUP\* 4.0b10 (Swofford 2002) was used to compute the uncorrected pairwise distances for all sequences (Tab. 2, Appendix II). We performed neighbour-joining (NJ), maximum parsimony (MP), maximum likelihood (ML) and Bayesian reconstructions. For ML and Bayesian analysis parameters of the model were estimated from the data set using Modeltest 3.7 (Posada & Crandall 1998) and MrModeltest 2.3 (Nylander 2002), respectively. For the MP analysis, we used the “heuristic search” with the “random addition” option of PAUP\* (Swofford 2002) with 10 replicates, using the TBR (tree bisection-reconnection) branch swapping option. For the ML tree we used the PhyML 3.0 computer cluster of the Montpellier bioinformatics platform (<http://www.atgc-montpellier.fr/phyml/>) (Guindon & Gascuel 2003). All Bayesian analyses were performed with MrBayes, version 3.12 (Huelsenbeck & Ronquist 2001). The exact parameters used for the Bayesian analyses followed those described in detail by Reeder (2003). For the Bayesian reconstruction clades with posterior probabilities (PP)  $\geq 95\%$  were considered strongly (significantly) supported. Additionally, we used bootstrap analyses with 1000 (for ML), 2000 (for MP) and 20000 (for NJ) pseudoreplicates to evaluate the relative branch support in the phylogenetic analysis.

In the morphological analysis measurements follow standard procedures (e.g. Werner 1902; Mariaux et al. 2008) and were taken on preserved material with an electronic dial calliper ( $\pm 0.1$  mm). All measurements are given in mm (Tab. 3, Appendix II). Analysis of morphological data has been performed using PAST software (Version 1.82b; Hammer et al. 2001). If measurements (e.g. femur length) differed between body sides, mean values were used. Photos of living specimen have been used to analyse colouration patterns.

Investigated specimens are deposited in Muséum d'histoire naturelle, Geneva (MHNG); Muséum national d'Histoire naturelle, Paris (MNHN); National Museum, Museum of Natural History, Prague (NMP6V); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin (ZMB); Zoologische Staatssammlung München (ZSM).

## RESULTS

To date ten taxa belonging to the genus *Trioceros* have been recognized in Cameroon (eight species + two subspecies), but the present phylogenetic analysis is inconsistent with this arrangement (Fig. 1). All four used phylogenetic methodologies strongly agree in the overall topology and in all cases support the same terminal clades. The phylogenetic analyses reveal only a single difference (discussed below) for the individual analysis of the two applied gene fragments (not shown), therefore, we only discuss the results of the combined analysis.

Distances between ingroup and outgroup species averaged 11.48% (10.58%–12.30%; Tab. 2, Appendix II). Interspecific distances within the ingroup ranged from 3.21%–6.90% excluding *T. oweni*.

*Trioceros oweni* is the most basal taxon in respect to all ingroup taxa, which are grouped within one clade fully supported in NJ, MP and ML, while still strongly, but not fully significantly supported in the Bayesian reconstruction (PP: 0.91). The main clade is divided into two major subclades with strong statistical support. The first subclade includes *T. camerunensis*, *T. cristatus*, and *T. montium*, but their mutual relationships remain unresolved. However, partly well supported substructure can be recognized within the two species, *T. montium* and *T. cristatus*. *Trioceros camerunensis* stands in a basal position to *T. montium*, but this is only significantly supported by the MP reconstruction. Within *T. montium*, we find a subdivision into three only slightly differentiated subclades. Overall the uncorrected *p*-distances of the included *T. montium* vouchers range between 0.00%–0.75%. Similarly, within *T. cristatus* a similar subdivision into three more distinct subclades is apparent. Here, the genetic distances between the included *T. cristatus* vouchers ranges between 0.00%–1.28%.

Contrary to the first major ingroup subclade, relationships of the species of the second major subclade remain unresolved and form a basal polytomy. Nonetheless, all terminal clades in this second major subclade are strongly supported and are well distinct regarding the individual branch lengths and bootstrap support for each terminal clade, mostly corresponding to currently accepted species within *Trioceros*. The morphologically very distinct taxon *T. eisentrauti* is grouped together with the two described *T. quadricornis* subspecies with uncorrected *p*-distance values of between 0.51%–1.08% between these three taxa. We found only one haplotype in each of the two subspecific taxa, *T. q. quadricornis* and *T. q. gracilior*, while in *T. eisentrauti* we uncovered a difference of two nucleotide substitutions in our newly gained sequences in comparison to the published 12S sequence of Pook & Wild

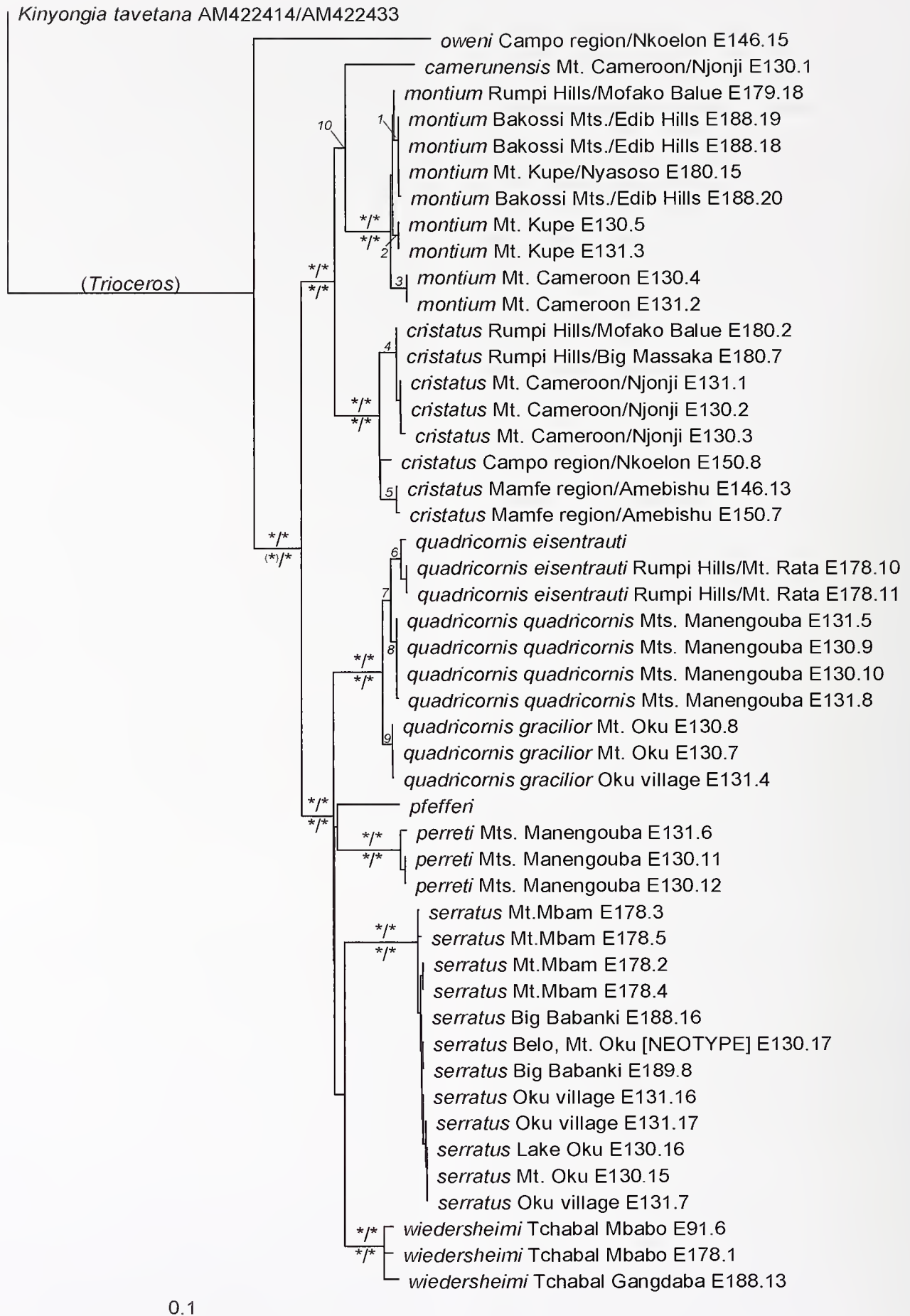
(1997). The distances of *T. eisentrauti* to the nominate form *T. q. quadricornis* (0.51%–0.64%) are about equal in size to the distances of the latter to *T. quadricornis gracilior* (0.63%–0.64%). The distance of *T. eisentrauti* to *T. quadricornis gracilior* is only moderately higher (1.02%–1.08%). These values are clearly within the intraspecific distance range of all included *Trioceros* species. Contrarily, the remaining taxa of this subclade show a much higher genetic differentiation between each other, ranging from 3.18%–5.00%. These other terminal clades correspond to the taxa *T. pfefferi* and *T. wiedersheimi*. The latter hornless taxon is represented by three genetically well differentiated clades. Two of them correspond to the two so far described subspecies, but we find a further significant split within the populations currently assigned to the nominate form.

## DISCUSSION

Following our molecular and morphological results several changes are necessary among Cameroonian chameleons of the genus *Trioceros*. The overall number of *Trioceros* taxa in Cameroon is raised to eleven and two already known taxa are revised in their taxonomic rank. Within the Cameroonian *Trioceros*, *T. oweni* is the most basal taxon, while the other taxa form two subclades, in which *T. camerunensis*, *T. cristatus*, *T. montium* form a lowland to submontane group while remaining taxa of the second subclade inhabit submontane to montane habitats (Pook & Wild 1997). Results and required changes will be discussed below in separate sections referring to the relevant species groups.

### *Trioceros oweni* (Gray, 1831) (Fig. 2A)

*Trioceros oweni*, the type species of the genus *Trioceros*, is the most basal in respect to all remaining Cameroonian taxa (Fig. 1). The value of uncorrected *p*-distance between *T. oweni* and the outgroup taxon *Kinyongia tavetana* (12.21%) is within the genetic distance range of all included *Trioceros* taxa to the outgroup (10.58–12.30%, Tab. 2, Appendix II). However, values of uncorrected *p*-distances between *T. oweni* and remaining Cameroonian *Trioceros* taxa (8.57–10.22%) are significantly higher than values in-between the remaining ingroup taxa (see Tab. 2, Appendix II), and the maximum distance value is only marginally lower than the minimum distance of all *Trioceros* to the outgroup taxon. Based on molecular data, Pook & Wild (1997) suggested that *T. oweni* might belong to a distinct species group, being closer related to *T. johnstoni*, an East African species, than to other western *Trioceros*. In the past, Werner (1902) grouped *T. oweni* together with *T. johnstoni*, *T. melleri* and *T. weneri*, while *T. cristatus*, *T. montium*, *T. pfefferi* and *T. quadricornis* be-



**Fig. 1.** Phylogram of the combined analysis of the 16S and 12S rRNA sequence fragments (49 sequences / 960 bp in total). The star symbol “\*” denotes significantly supported nodes. [The values for the internal nodes are as follows (NJ/MP/PP/ML, respectively): 1:(78/61/0.78/73); 2:(95/98/1.00/96); 3:(99/87/0.99/99); 4:(100/98/1.00/100); 5:(100/93/1.00/100); 6:(86/96/1.00/92); 7:(81/89/0.82/86); 8:(97/67/0.56/94); 9:(100/89/0.97/99); 10:(69/83/0.61/63)].

longed to a different morphological group. A simple BLAST search in GenBank, performing a similarity check of sequences, of the applied *T. oweni*-sequence identified *T. melleri* (16S) or *T. sternfeldi* (12S) to show the highest similarity values; both again East African species. According to Townsend & Larson (2002) and Tilbury & Tolley (2009), *T. melleri* is related to *T. johustoui*. While the only western *Trioceros* (*T. feae* from Bioko Island, Equatorial Guinea) in the study of Tilbury & Tolley (2009) is placed basal to all other *Trioceros*. Similarly, Townsend & Larson (2002) found that all western *Trioceros* (including *T. feae*) studied by them stand as a sister clade to the other members of the genus.

Hence, concerning *T. oweni* our results support the view of Pook & Wild (1997) that *Trioceros* taxa in western Central Africa are more closely related to each other than to *T. oweni*. The exact position of *T. oweni* remains to be assessed in future studies with a wider sampling from the whole distribution area of this genus.

#### Lowland-submontane clade

##### *Trioceros camerunensis* (Müller, 1909) (Fig. 2B)

In the past Mertens (1964) classified *T. camerunensis* as a subspecies of *T. montium* based on morphological similarities and zoogeographical affinity, but Klaver & Böhme (1992) reclassified the taxon as a valid species. Our molecular results do support close relationships between *T. camerunensis* and *T. montium* but also confirmed its full species status. According to Pook & Wild (1997), *T. camerunensis* is more closely related to *T. feae* (not included in our study) than to *T. montium*.

#### Lowland-submontane clade

##### *Trioceros montium* (Buchholz, 1874) (Fig. 2C)

Within the well supported monophyletic *T. montium*-clade, distinct subclades appear (Fig. 1; Tab. 2, Appendix II). Buchholz (1874) described *T. montium* from Bonjongo, Mt. Cameroon. Later Mertens (1938) described a subspecies *T. montium grafi* from Mongonge, on the opposite side of Mt. Cameroon. Klaver & Böhme (1992) regarded it only as an aberrant form and moved it in synonymy with the nominate form. Based on dorsal crest shape, Perret & Mertens (1957) indicated a possible subspecies from the Manengouba Mts. but, as in *T. m. grafi*, Klaver & Böhme (1992) proved the occurrence of this character to be more widespread. However, Pook & Wild (1997) mentioned differences in the courtship livery of *T. montium* between populations. Differences in colouration are of importance in species recognition and may play a role in character displacement (Pook & Wild 1997; Rand

1961; Wagner et al. 2009b) but further studies on this aspect are required. *Trioceros montium* inhabits the submontane zone of Mt. Cameroon, Rumpi Hills, Manengouba Mts. area and parts of the south-western edge of the Bamenda Highlands (Gonwouo et al. 2006). At first glance no morphological characters indicate a separation of populations. Hence, we refrain to draw any premature conclusions at this point.

#### Lowland-submontane clade

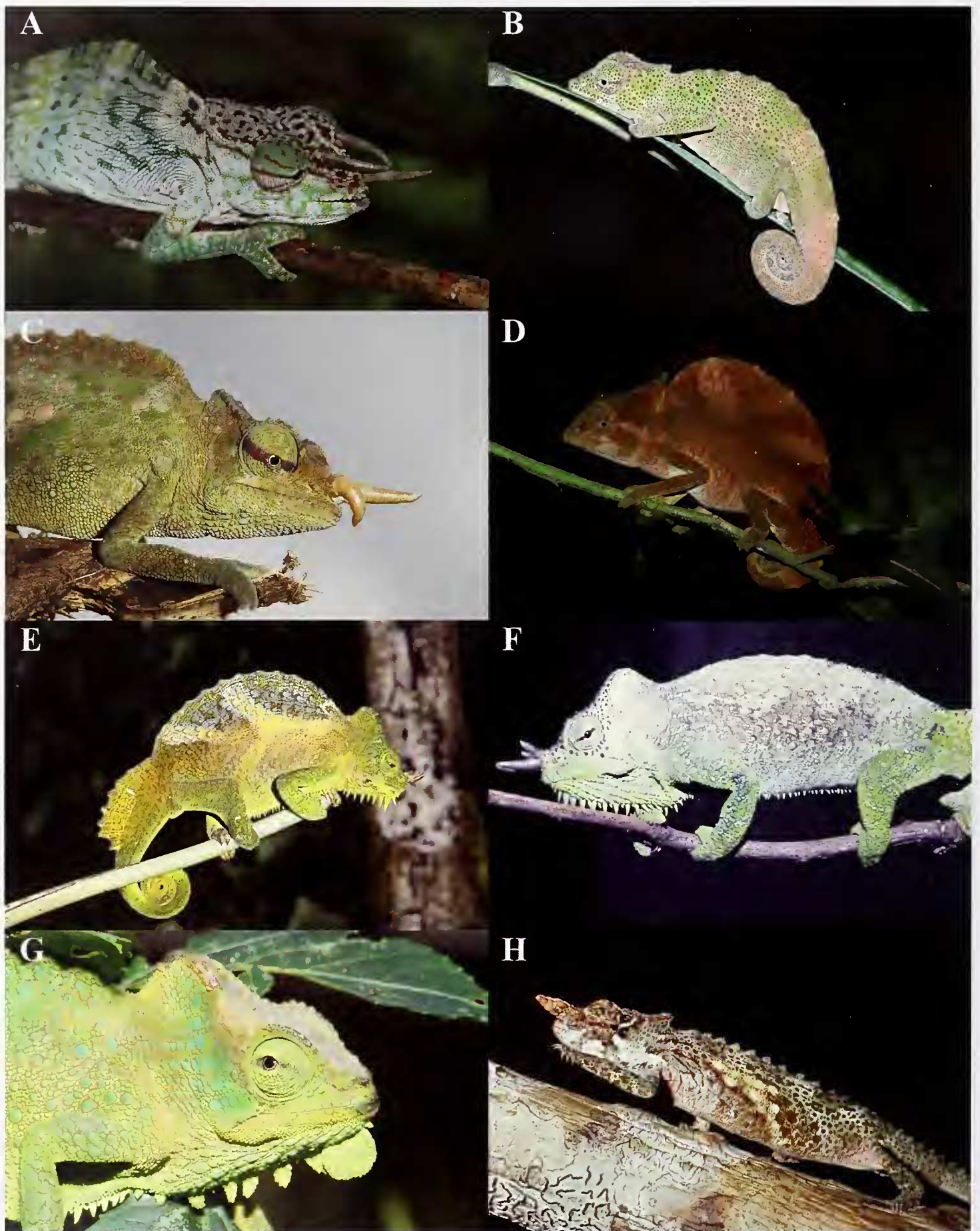
##### *Trioceros cristatus* (Stutchbury, 1837) (Fig. 2D)

A similar situation appears in *T. cristatus* and distinct subclades are detectable within this taxon and as in the preceding case, uncorrected *p*-distances show only comparatively low differences between the clades (Fig. 1; Tab. 2, Appendix II). Stutchbury (1837) described *T. cristatus* from Gabon and since then no further subspecies have been described or taxa synonymised with *T. cristatus*. *Trioceros cristatus* is widespread in the lowland to submontane zone from Nigeria to the Central African Republic, Gabon and the Republic of the Congo (Klaver & Böhme 1992; Pauwels & Vande weghe 2008). Furthermore, the species has been reported from Ghana and Togo (see references in Klaver & Böhme 1992) but, these localities must be regarded with caution, as they have not been confirmed recently. In contrast to *T. montium* the species is more widespread. A more detailed analysis of the overall distribution must be applied before any conclusions can be drawn.

#### Submontane-montane clade

##### *Trioceros quadricornis* (Tornier, 1899)-group (Figs 2E–G), including *Trioceros quadricornis eisen-trauti* (Mertens, 1968) NEW RANK

Molecular results require changes in the former *quadricornis*-group. Morphological distinctness (body size, shape of dorsal crest, number and size of rostral horns, lung morphology) between populations from southern parts of the Cameroon mountain chain (Mt. Kupe, Manengouba Mts.) and northern parts (Bamenda Highlands to Obudu Plateau in eastern Nigeria) have already been recognized by Böhme & Klaver (1981). Uncorrected *p*-distance values between the taxa *quadricornis* and *gracilior* (Tab. 2, Appendix II), indicate a very recent split and these taxa correspond to subspecies. *T. q. gracilior* is known from the Bamboutos Mts, Mbulu Hills, Mt. Lefo, Mt. Oku and the Obudu Plateau, while *T. q. quadricornis* is present on Manengouba Mts. and Mt. Kupe (Böhme 1975; Böhme & Klaver 1981; Gonwouo et al. 2006; Joger 1982; Klaver & Böhme 1986, 1992).



**Fig. 2.** Cameroon chameleons (in life): A = *Trioceros oweni* male (Campo region; photo by J.A.M. Wurstner). B = *T. camerunensis* (Njonji, Mt. Cameroon). C = *T. montium* male; specimen with an aberrant horn shown (Big Massaka, Rumpi Hills). D = *T. cristatus* male (Nkoelon, Campo region). E = *T. q. quadricornis* male (Mt. Kupe). F = *T. q. gracilior* male (Mt. Lefo; photo by W. Böhme). G = *T. q. eisentrauti* female (Mt. Rata, Rumpi Hills). H = *T. pfefferi* male (Kodmin, Bakossi Mts.).

We group the morphologically highly distinct taxon *T. eisentrauti* as a distinct subspecies of *T. quadricornis* (Fig. 1), a position already indicated by Pook & Wild (1997). But, while in the latter publication and in our 12S-only analysis (not shown) *eisentrauti* is placed as the basal sister taxon to the two *T. quadricornis* subspecies, according to our combined results (16S, 12S) this is not the case. Despite its morphological uniqueness (gular crest formed of flaps in *eisentrauti* and a gular crest formed of conical scales in other *Trioceros* taxa), molecular results reveal close relationships between these three taxa with values of uncorrected *p*-distances within intraspecific ranges. Values of uncorrected *p*-distances between *eisentrauti* and *T. q. quadricornis* are comparable to values between the *T. quadricornis* subspecies and values are only marginally higher between *eisentrauti* and the subspecies *T. q. gracilior* (Tab. 2, Appendix II). However, the taxa show a disjunct distribution with *T. q. quadricornis* occurring in the Manengouba area (see above) and *T. eisentrauti* being endemic to the Rumpi Hills in western Cameroon (Gonwouo et al. 2006; Klaver & Böhme 1997). All taxa inhabit pristine montane habitats, *T. q. quadricornis* occurring at altitudes between 1.800–2.250 m a.s.l., *T. q. gracilior* at altitudes between 1.800–2.400 m a.s.l. and *T. eisentrauti* in altitudes above 1.150 m a.s.l., respectively (Gonwouo et al. 2006; Pook & Wild 1997). We have located *T. eisentrauti* on Mt. Rata in the Rumpi Hills only above 1.600 m a.s.l., hence, it is probably even more restricted in its altitudinal and overall distribution range than previously indicated. In the original description of *T. eisentrauti* Mertens (1968) had already indicated relatedness to *T. quadricornis* taxa according to body size and shape of the dorsal and tail crests. Böhme & Klaver (1981) emphasized the similarities of *T. q. quadricornis* and *eisentrauti* in comparison to *T. q. gracilior* and remarked that rostral tubercles in *eisentrauti* might represent reduced rostral horns, which are present in *T. q. quadricornis* (up to two pairs of rostral horns) and *T. q. gracilior* (up to three pairs of rostral horns). However, reduction of rostral horns is also known in *T. q. quadricornis* and *T. q. gracilior* (Böhme & Klaver 1981; Mertens 1968) and Böhme & Klaver (1981) assumed that reduced horns represent a more derived character state. From the genetic point of view, we are aware that the low genetic differentiation in mitochondrial DNA might be in some cases caused by introgressive hybridization in the evolutionary history of two species. However, we believe that the similar overall morphology (body shape and size, shape of the crests) of *T. quadricornis* and *eisentrauti* also further supports our hypothesis of two closely related, but conspecific taxa. Due to the constant morphological differences between them and their allopatric distributions we regard the taxa *quadricornis* and *eisentrauti* as subspecies of a single species. *Trioceros quadricornis quadricornis* (Tornier, 1899) from the Manengouba area represents the nominate form

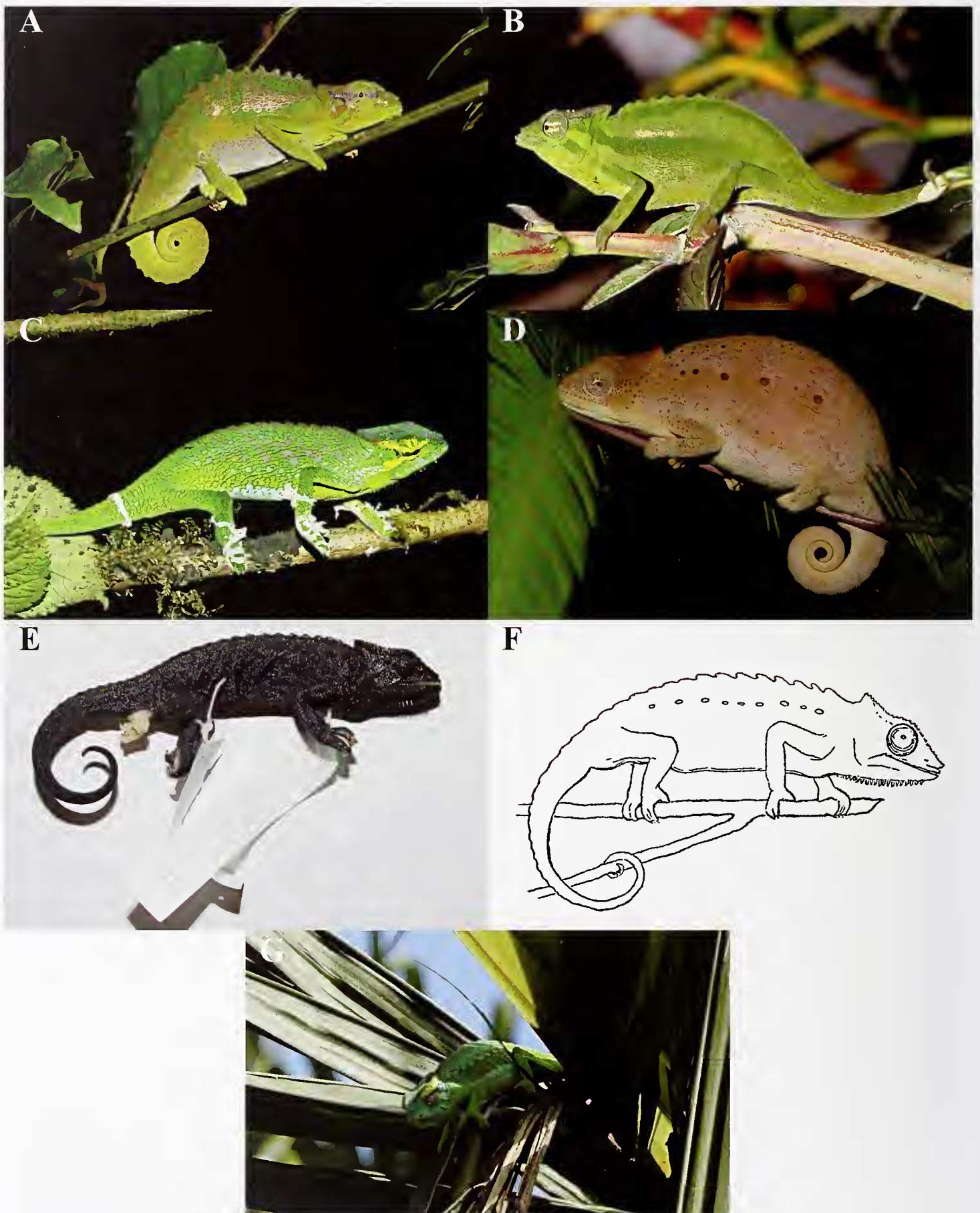
while the taxon *eisentrauti* from the Rumpi Hills is given a new systematic status *Trioceros quadricornis eisentrauti* (Mertens, 1968) NEW RANK. In contrast to the afore discussed species (*T. montium* and *T. cristatus*), any contact zone between these two allopatric taxa can be excluded due to their highly restricted altitudinal distribution. As above, low genetic differences suggest a very recent split presumably connected to the altitudinal range shifts of the lower-temperature forests up to the mountains after the end of the Pleistocene Ice Ages (when montane forests in the tropics expanded to the lower elevations; Hewitt 2004). All three subspecific taxa of *T. quadricornis* could now represent species *in statu nascendi*.

#### Submontane-montane clade

#### *Trioceros wiedersheimi* (Nieden, 1910)-group (Figs 3A–G), including *Trioceros perreti* (Klaver & Böhme, 1992) NEW RANK

Further changes are necessary within the former *wiedersheimi*-group. Klaver & Böhme (1992) described the subspecies *T. w. perreti* from Manengouba Mts. Molecular results however reveal full species status for this taxon, as the uncorrected *p*-distances between *T. wiedersheimi* populations from Manengouba Mts. and populations further north (Bamenda area, Tchabal Mbabo) are clearly within the interspecific range of other western *Trioceros* species (Tab. 2, Appendix II). We thus herein elevate the taxon to the full species rank: *Trioceros perreti* (Klaver & Böhme, 1992) NEW RANK. The present distribution of *T. perreti* covers the Manengouba Mts. and the Bakossi Mts. (Euskirchen et al. 2000; Gonwouo et al. 2006).

Regarding the former nominate *T. w. wiedersheimi*, molecular and morphological results lead to recognition of two distinct clades with uncorrected *p*-values within interspecific range of this genus (Tab. 2, Appendix II). Formerly, *T. w. wiedersheimi* has been thought to occur in Cameroon north of the Manengouba Mts. (inhabited by *T. perreti* (Klaver & Böhme, 1992), see above). It has been found along the Cameroon mountain chain (Bamboutos Mts., Mbulu Hills, Mt. Lefo, Mt. Mbam, Mt. Oku and Mt. Tchabal Mbabo) and in eastern Nigeria (Gotel Mts., Mambilla Plateau and Obudu Plateau), where it inhabits montane savannas and grasslands between 1400 and 2450 m a.s.l. (Böhme & Nikolaus 1989; Chirio & LeBreton 2007; Dunger 1967; Gonwouo et al. 2006; Herrmann et al. 2006; Klaver & Böhme 1992). Nieden's (1910) description of *T. wiedersheimi* is based on two specimens, a female from Genderogebirge (=Tchabal Mbabo) and a subadult male from the village Tsch'a (Bekom), Bamenda area. In the course of describing *T. w. perreti*, Klaver & Böhme (1992) designated the female specimen as lectotype and consequently restricted the type locality to the Genderogebirge



**Fig. 3.** Cameroon chameleons (in life): A = *Trioceros wiedersheimi* male (Mt. Tchabal Gangdaba). B = *T. perreti* male (Kodmin, Bakossi Mts.). C = *T. serratus* male (Kedjom Keku = Big Babanki, Bamenda Highlands). D = *T. serratus* female (Kedjom Keku = Big Babanki, Bamenda Highlands). E = Male neotype of *T. serratus* (in alcohol; MNHN 2007.1494; Belo, Mt. Oku). F = Illustration of *T. serratus* after Mertens (1922; "Südkamerun"). G = Male neotype of *T. serratus* (in life; MNHN 2007.1494, Belo, Mt. Oku) in situ.



(=Tchabal Mbabo). As one of the uncovered molecular clades contains specimens from Tchabal Mbabo, topotypic material, thus this clade should correspond to *T. wiedersheimi*. The occurrence of *T. wiedersheimi* on Tchabal Gangdaba has already been assumed in the past (Chirio & LeBreton 2007; Klaver & Böhme 1992) and we can confirm its occurrence on this mountain range. Thereafter, the species is known from the northernmost parts of its former assumed distribution, while populations of the southern molecular clade from the Bamenda Highlands, Mt. Mbam, and Mt. Oku represent a distinct taxon. It is also very likely that this clade covers populations from the Mbulu Hills, Mt. Lefo and the Obudu Plateau in southern Nigeria as this would correspond to a bordering range from other studies (Gonwouo et al. 2006). Solely one locality in direct proximity north of the Manengouba Mts. (see map in Gonwouo et al. 2006) appears uncertain, as *T. perreti* has been regarded as restricted to the mountain range, but the specimen was not available to us for this study.

Mertens (1922) described *Chamaeleon serratus* from "Südkamerun" (= South Cameroon, Fig. 3F), being most similar to *T. wiedersheimi*, but differing by size, prominence of the temporal cristae and course of the lateral cristae (Fig. 3E). The species has been later synonymized with *T. wiedersheimi* by Mertens himself (1940; see below). Klaver & Böhme (1992) argued that *T. serratus* is a synonym of *T. wiedersheimi*, as the original description, especially the low number of scales on the scalloped dorsal ridge, is not consistent with *T. perreti* from Manengouba Mts. A comparison with the type specimen of *T. serratus* was not possible, as the type specimen was probably destroyed during the Second World War (H. Wermuth 16.4.1979 in litt., in Klaver & Böhme 1992).

Mertens (1922) rightly suggested that *T. wiedersheimi* is morphologically the most similar species to *T. serratus*, but obviously he only compared his material with Nieden's (1910) original description and not with the type specimen, as he only cited the original sections for comparison. Beside the characters cited above, Mertens (1922) mentioned that no additional distinct characters like the shape of the dorsal crest, which is at the origin of the specific name (Mertens 1968), are given in Nieden's (1910) description. [Remark: Nieden (1910) stated that a dorsal crest is lacking but, a dorsal midline is formed of two rows of tubercle scales which are separated in groups of 3–4 scales in the male specimen from the Bamenda region].

Later, Mertens (1940) reported on a collection delivered by M. Köhler including chameleons from the Bamenda Highlands (four males + two females) and concluded that *T. serratus* is in fact a junior synonym of *T. wiedersheimi*. His conclusion was based on the fact that males of the

new material corresponded to the "paratypoid" (= paratype) of *T. serratus*, while females are consistent with the female cotype (=syntype) of *T. wiedersheimi* and finally he recognized that the prominence of the lateral and temporal cristae is subject to individual variation. In a subsequent publication on material collected by Eisentraut at Lake Oku and Lake Manengouba, Mertens (1968) confirmed his former statement and remarked that males in *T. wiedersheimi* also do possess a serrated dorsal crest, while the dorsal crest is straight and simple in females. With the exception of Lake Manengouba (recognized as distinct by Klaver & Böhme 1992), all localities of the material examined by Mertens belong to the newly discovered southern clade.

Our morphological analysis of material throughout the distribution range of the former taxon *T. w. wiedersheimi* revealed that distinguishing characters chosen by Mertens (1922) are hard to assign to members of one clade, as many characters are present in members of both clades (lack of heel spur, lack of occipital lobes, etc.) separating them from other taxa. Of the three main characters given by Mertens (1922), two of them seem to be inapplicable. According to Mertens (1922): (a) *T. serratus* grows larger than *T. wiedersheimi*, but four of ten males from Tchabal Mbabo and the Gotel Mts. (= *T. wiedersheimi*) possess a larger body length than the largest member of the southern clade, and the largest female also belongs to *T. wiedersheimi*; (b) temporal cristae are distinct in *T. wiedersheimi* and indistinct in *T. serratus*, but this character varies within both clades (Fig. 4), which was already mentioned for Bamenda populations by Mertens (1940); and (c) Mertens (1922) differentiated the course of the lateral cristae (in front of the eye first running along the eye then in a weaker slope to the tip of the snout in *T. wiedersheimi*, in contrast to an even slope in direction to the tip of the snout in *T. serratus*) and this character is clearly more applicable to specimens belonging to the southern, previously unrecognized clade (Fig. 4). Nonetheless, with just a few specimens of each clade a determination on this character alone is difficult. At last, the name-giving character, a serrated dorsal crest is also present in males of both clades. The number of scale rows forming the crenulation is consistent in both clades (being formed of up to three rows of scales) and the extent of crenulation along the dorsum and base of tail also varies in both clades. According to Mertens (1922) each cusp of the crenulation is 3 mm high and 4.5 mm long, but only in one very large specimen of *T. wiedersheimi* a comparable size has been reached, while specimens of similar size to Mertens' (1922) specimens possess smaller cusps in both clades. The given type locality "Südkamerun" does not allow any direct localization of *T. serratus*. Moreover, the subadult male paralectotype of *T. wiedersheimi* originates from the Bamenda area (part of the southern clade) and might have



**Fig. 4.** Heads in lateral view. Row 1–3: *Trioceros wiedersheimi* (from left to right): ZMB 21873 female (lectotype), ZFMK 75744 female, ZFMK 68943 male, ZFMK 75740 male, ZMB 21857 male, ZMB 74805 female, ZFMK 78714 male, MNHN 2005.2753 male, NMP6V 74112 male, ZFMK 75745 female, MHNG 1544.001 male, MHNG 1544.002 male. Row 4–6: *T. serratus* (from left to right): MNHN 2007.1494 male (neotype), MNHN 2007.1465 female, NMP6V 74104 male, MHNG 1365.023 female, ZSM 13.1925 subadult male, MNHN 2007.1464 male, ZFMK 5801 male, MNHN 2007.1463 male, MNHN 2007.1461 female, MHNG 1365.024 female, MHNG 1010.049 male, ZFMK 5800 female.

understandably mistaken as part of the distribution of *T. wiedersheimi*. The distribution of the southern clade covers the main part of former distribution of *T. wiedersheimi* and makes it more plausible to be termed “Süd-kamerun” (South Cameroon) in comparison to the Tcha-bal Mbabo area. Of Mertens (1922), most informative characters, the only reasonably useful for the recognition of *T. serratus* is the course of the lateral cristae. A course corresponding to Mertens’ (1922) information is present in members of the southern clade.

According to Article 75 of the International Code of Zoological Nomenclature (ICZN 1999) a neotype is required when no name-bearing types are believed to be extant and it is necessary to define a taxon objectively. In our case, a designation of a neotype is necessary because the holotype is lost (H. Wermuth 16.IV.1979 in litt., in Klaver & Böhme 1992; A. Schlüter, herpetological curator of the SMNS, in litt. 8.III.2010) and the taxon requires unambiguous clarification of its taxonomic status. The type locality of the taxon is now set as the collecting locality of the neotype (Article 76 in ICZN 1999). Hence, we here revalidate *T. serratus* and provide a description of the neotype at the end of this section.

#### Submontane-montane clade

##### *Trioceros pfefferi* (Tornier, 1900) (Fig. 2H)

According to Townsend & Larson (2002) *T. pfefferi* is related to (what these authors termed) *T. quadricornis* and *T. wiedersheimi*, but more closely to the latter species. While the 12S-only analysis of Pook & Wild (1997) also suggested a grouping of *T. pfefferi* and *T. wiedersheimi*, an unambiguous position of this rare taxon was not possible in our analysis with the combined 16S+12S-gene fragments (see Fig. 1). Further, because of the lack of a working 12S sequence for the sample of *T. pfefferi* that we used, we used a chimera-sequence consisting of the original 12S data as published by Pook & Wild (1997; only available in the original publication, not in GenBank) and our new 16S data of another specimen. Therefore, all that can be said for now is that *T. pfefferi* is more closely related to the taxa of the hornless *T. wiedersheimi*-complex than to *T. montium* or *T. quadricornis*, which share morphological characters like horns with *T. pfefferi*. It is also interesting to underline that the horned species, *T. montium*, *T. quadricornis* and *T. pfefferi*, do not form a monophyletic clade, and thus, horns evolved several times in the evolutionary history of the western *Trioceros* species group.

Regarding the overall distribution of *T. pfefferi*, this species shows a similar distribution pattern to two other species groups (a) *T. perreti* – *T. serratus* – *T. wiedershei-*

*mi* and (b) *T. q. quadricornis* – *T. q. gracilior*. Both groups show a rough distribution with one taxon in the Manengouba area and a second one in the Bamenda Highlands (additionally a third in the northernmost parts in the case of *T. wiedersheimi*). As in both these groups former allopatric populations have been recognized as valid taxa, the recently discovered populations of *T. pfefferi* from Mbulu Hills and Ediango (see Gonwouo et al. 2006) should be compared to southern populations in future studies, especially as the species also inhabits submontane/montane altitudes between 1100–1800 m a.s.l. and might show a disjunct distribution, as well.

Noteworthy is, that present distribution data reveal a disjunct partitioning of montane areas in the Cameroon mountain chain with related taxa (with the exception of *T. pfefferi*, but see above) but apparently the highest peak (Mt. Cameroon) does not possess an endemic montane taxon. Only the submontane *T. montium* is present on Mt. Cameroon and elevations further north, but this taxon requires further studies to understand a potential distributional separation (see above).

#### Designation of neotype and redescription of *Chamaeleon serratus* Mertens, 1922 (now considered as a member of the genus *Trioceros* sensu Tilbury & Tolley 2009)

**Holotype (lost).** *Chamaeleon serratus* Mertens (1922), Zool. Anz., 54: 191. Mus. Stuttgart, Nr. 4640 (male), probably destroyed during the Second World War (H. Wermuth 16.4.1979 in litt., in Klaver & Böhme 1992; A. Schlüter, herpetological curator of the SMNS, in litt. 8.3.2010), type locality: „Süd-kamerun“.

**Neotype.** MNHN 2007.1494, adult male with everted hemipenes. Collected by Ivan Ineich on 9 May 2007 on a palm tree near road border of the road from Anyajua to Belo, close to Belo, Mt. Oku, Cameroon. Coordinates: N 06°10'32" E 10°21'09" (Lat.: 6.17547°, Lon.: 10.35244), 1339 m (4394 feet) a.s.l.

**Type locality.** Belo, Mt. Oku, Cameroon

**Distribution.** Cameroon, Nigeria

**Additional material examined** (Appendix I)

**Diagnosis.** *Trioceros serratus* differs from all other *Trioceros* except *T. wiedersheimi* and *T. perreti* by a crest formed by the canthi rostrales merging above the snout, forming a depression between the tip of the snout and the merged crest. Moreover, it can be distinguished from *T. q. eisentrauti* by the absence of gular flaps (Fig. 2D), from *T. montium*, *T. oweni*, *T. q. quadricornis*, *T. q. gracilior*

and *T. pfefferi* by the absence of rostral appendages in male specimens (Figs 2A, 2C, 2E–F, 2H) and from *T. camerunensis* and *T. cristatus* by the presence of a gular crest (Figs 2B, 2D).

*Trioceros serratus* can be differentiated from *T. wiedersheimi* by a combination of the following characters: *T. serratus* tends to stay smaller than *T. wiedersheimi* and the tail length / body length ratio is lower in *T. serratus* (Tab. 3, Appendix II): total body length, *T. wiedersheimi* (max. total length in males: 208 mm; in females: 172 mm) growing larger than *T. serratus* (max. total length in males 179 mm; in females 158 mm), but this observation is not statistically significant (in males:  $p > 0.05$   $N_{T.w.}=10$ ,  $N_{T.s.}=27$ ; in females:  $p > 0.05$   $N_{T.w.}=8$   $N_{T.s.}=15$ ); mean tail length / body length ratio is significantly higher in *T. wiedersheimi* (in males:  $p < 0.05$   $N_{T.w.}=10$ ,  $N_{T.s.}=27$ ; in females:  $p < 0.05$   $N_{T.w.}=8$   $N_{T.s.}=15$ ); the mean numbers of flank scales at midbody, although values overlap, the number of flank scales at midbody is significantly higher ( $p < 0.01$ ) in *T. serratus* ( $N=44$ ; range: 56–76, mean: 66) than in *T. wiedersheimi* ( $N=19$ ; range: 57–68, mean: 62); number of scales between the eye and the end of the head is significantly higher ( $p < 0.001$ ) in *T. serratus* ( $N=44$ ; range: 6–11, mean: 8) than in *T. wiedersheimi* ( $N=19$ ; range: 5–9, mean: 7) and single scales tend to be distinctly larger in *T. wiedersheimi* (Fig. 4); the course of the lateral cristae in front of the eye, decreases almost steadily from the eye to the tip of the snout in *T. serratus*, while it first runs along the eye and then, from a point approximately at the middle of the eye, in a lower slope to the tip of the snout in *T. wiedersheimi*.

*Trioceros serratus* can be differentiated from *T. perreti* by a combination of the following characters: total body length of similar size but, although largest specimens belong to *T. serratus*, the mean total length is slightly higher in *T. perreti* (in males:  $p > 0.05$   $N_{T.p.}=25$ ,  $N_{T.s.}=27$ ; in females:  $p > 0.05$   $N_{T.p.}=10$ ,  $N_{T.s.}=15$ ); mean tail length / body length ratio is significantly higher in *T. serratus* in males ( $p < 0.05$   $N_{T.p.}=25$ ,  $N_{T.s.}=27$ ) lower, but not significantly, in females ( $p > 0.05$   $N_{T.p.}=10$   $N_{T.s.}=15$ ); mean numbers of flank scales at midbody, although values clearly overlap, the number of flank scales at midbody is significantly lower ( $p < 0.001$ ) in *T. serratus* ( $N=44$ ; range: 56–76, mean: 66) than in *T. perreti* ( $N=36$ ; range: 65–86, mean: 74; in one single specimen even 93); number of scales between the eye and the end of the head is significantly lower ( $p < 0.001$ ) in *T. serratus* ( $N=44$ ; range: 6–11, mean: 8) than in *T. perreti* ( $N=37$ ; range: 9–15, mean: 11), scales behind the eyes are of similar size to flank scales in *T. perreti* and slightly enlarged in *T. serratus*; maximum length of gular crest is significantly higher in *T. serratus* than in *T. perreti* (in males:  $p < 0.001$   $N_{T.p.}=25$ ,  $N_{T.s.}=27$ ; in females:  $p < 0.001$   $N_{T.p.}=12$ ,

$N_{T.s.}=17$ ); length of mouth gap / distance mouth gap to tip of helmet ratio is significantly higher in males of *T. serratus* ( $p < 0.05$ ;  $N_{T.p.}=25$ ,  $N_{T.s.}=27$ ), while the value is not significant in females ( $p > 0.05$ ;  $N_{T.p.}=12$ ,  $N_{T.s.}=17$ ); dorsal part of the casque flat in *T. serratus* (and *T. wiedersheimi*) and convex in *T. perreti* (Böhme & Klaver 1992). For morphometrics see Tab. 3, Appendix II.

**Description of the neotype.** Adult male in good condition; body shape slender, laterally compressed; body length (measured from snout tip to cloaca) 83.0 mm; tail length 76.0 mm; tail base swollen and both hemipenes everted (Fig. 3F); vertical eye diameter 7.0 mm; canthus parietalis formed of 7 scales, measuring 6.8 mm (few additional slightly rough and ridged scales cranially of the parietal crest); distance snout tip to tip of helmet 24.3 mm; rostral crest merging above snout tip; rostral appendages absent; lateral and temporal crest distinct, both crests fusing posteriorly; occipital lobes absent; length of mouth gap 12.3 mm, mouth slightly opened; throat with fine longitudinal grooves between scale rows; gular crest present, formed of 24 scales, max. length of gular crest scale 1.7 mm, gular crest passing into ventral crest; lateral head scales behind eye enlarged in comparison to flank scales; lateral body scalation subhomogeneous but with interposed enlarged scales; dorsal crest present, serrated, formed out of 2–4 scales, diminishing in height caudally, scales of dorsal crest larger than flank scales; scales on extremities and tail (laterally and ventrally) of similar size as on body; fingers terminate in a single claw; hind feet without tarsal spurs.

Colouration in live (Fig. 3G): general body colouration greenish, enlarged scales on flanks pale brown, lateral and upper side of head pale bluish, upper eye border bright yellow, gular region green, upper most part of flanks and lower flank pale blue.

Colouration in alcohol (Fig. 3E): head and body dark greyish, gular crest of the same colour as body, ventral crest pale grey; sole of foot and palm of hand whitish; everted hemipenes whitish.

**Variation.** The number of interposed enlarged scales on flanks vary in number per line and also in number of lines. Length of gular crest scales and their number is quite variable (Tab. 3, Appendix II). Comparing the sexes, males show a higher body length – tail ratio than females and longer scales forming the gular crest (Tab. 3, Appendix II). Females generally possess a dorsal ridge, the dorsal midline is slightly serrated in one specimen (MNHN 1998.0415) forming an indistinctly serrated dorsal crest.

**Colouration.** The general ground coloration tends to be greenish or brownish. Enlarged scales on the flanks tend

toward being brown or blue and more conspicuous (Figs 3C–D). A bright stripe of differing colouration runs from the anterior part of the eye (or even starts in front of the eye) and splits into rays of colour on the eyelid; one of them running backwards along the temporal crest or between the temporal and lateral crest (Figs 3C, G). As in *T. wiedersheimi* the venter is brighter than the flanks and is pale blue or a lighter green / brown in living specimens (Fig. 3C). Blue colouration may be scattered around the mouth gap, on the top of the head, and on the flanks. The ventral line is whitish. In alcohol colourations fade away and specimens turn either pale grey-bluish (leaving some of the brighter rays on the eye visible) or turn dark and colours disappear almost completely.

**Distribution.** The species is known to occur in Cameroon and Nigeria. Within Cameroon it inhabits montane savannahs in the Bamenda Highlands and Mt. Mbam, and in Nigeria it has been reported from the Obudu Plateau (Böhme 1975; Akani et al. 2001). In contrast, reports from the Gotel Mts in Nigeria (Böhme & Nikolaus 1989) can be referred to *T. wiedersheimi*.

**Genetics.** The genetic comparison for the uncorrected *p*-distances of the combined mitochondrial 16S+12S rRNA fragments (Tab. 2, Appendix II) with the two morphologically most similar species *T. wiedersheimi* and *T. perreti* gave the following results: interspecific comparison between *T. serratus* and *T. wiedersheimi* ranged between 3.22%–4.08%, while the intraspecific variation within *T. serratus* was much lower at 0.00%–0.42% (N= 12). The interspecific difference between *T. serratus* and *T. perreti* ranges from 4.33%–4.86%, while those between the taxa *T. perreti* and *T. wiedersheimi* reach 3.74%–4.13%.

**Natural history remark:** Six gravid females contained the following numbers of eggs: 7, 8 (x2), 9 (x2) and 11. Size of measured eggs (N=10) ranges between 13.0–15.0 x 7.7–8.3 mm. In contrast, Angel (1940) reported ten eggs in a gravid female from the Mt. Bamboutos of 8 x 7 mm in size, which have been most probably not fully developed.

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**Appendix I**

## List of examined specimens

***Trioceros serratus* (Mertens, 1922)**

MNHN 2007.1494 (male neotype), Cameroon, Mt. Oku, border of the road from Anyajua to Belo (near Belo, at low altitude), date 9.V.2007, coll. I. Ineich; MHNG 964.037 (male), Cameroon, Bamenda, Kishong, 1.II.1939, coll. J.-L. Perret & R. Mertens; MHNG 1010.049-50 (2 males), Cameroon, Bafoussam, Bangwa, 1959, coll. J.-L. Perret; MHNG 1365.010 (male), Cameroon, Foumban, Mt. Nkogam, III.1969, coll. J.L. Amiet; MHNG 1365.019 (male), Cameroon, Bamiléké, Foto, XI.1972, coll. J.L. Amiet; MHNG 1365.023-24 (2 females), Cameroon, Dschang, Foto, XI.1972, coll. J.L. Amiet; MNHN 1997.3642 (male), Cameroon, Oku village, V.1997, coll. L. Chirio; MNHN 1998.0415, Cameroon, Lake Oku, altitude 2200 m, 7.VI.1998, coll. L. Chirio; MNHN 1998.0416-19, Cameroon, Mt. Oku, altitude 2000-2500 m, 25.VI.1998, coll. L. Chirio; MNHN 1998.0425, MNHN 1998.0429, Cameroon, Mt. Oku, altitude 2000-2500 m, 25.VI.1998, coll. L. Chirio; MNHN 2005.2781-2787, MNHN 2005.2900 (5 males + 3 females), Cameroon, Mt. Oku, Simonkuh, 10.572°E/6.234°N, altitude 2109 m, 8.VII.2002, coll. Programme CamHerp; MNHN 2005.2788 (male), Cameroon, Oku village, 19.IV.2000, altitude 2000 m, 10.505°E/6.202°N, coll. Programme CamHerp; MNHN 2007.1461-64 (2 males + 2 females), Cameroon, Mt. Oku area, around village of Elak Oku, 6.2441°N/10.5076°E, altitude 6474 ft, 6.V.2007, coll. I. Ineich & N. Lhermitte-Vallarino; MNHN 2007.1465 (male), Cameroon, Mt. Oku area, Lake, 6.2019°N/10.4609°E, altitude 7456 ft, 8.V.2007, coll. I. Ineich & N. Lhermitte-Vallarino; NMP6V 74104 (male), Cameroon, Kedjom Keku (= Big Babanki), Bamenda Highlands, 6°06.968'N 10°15.760'E, 1290 m a.s.l., 9.XI.2009, coll. V. Gvoždík; ZFMK 5798-5801 (2 males + 2 females), Cameroon, Lake Oku, 20-30.I.1967, coll. M. Eisentraut; ZFMK 15283 (male), Cameroon, Mt. Lefo, 5.-11.X.1974, coll. W. Böhme & W. Hartwig; ZFMK 18105-6, ZFMK 18108 (male + 2 females), Cameroon, Mezam, Bafout, 1975-76, coll. P. Shu Mfosono; ZMB 21860 (female), Cameroon, Bamenda, no date; ZMB 24909 (male), Cameroon, Bamenda, coll. Adametz; ZSM 13/1925 (male), Cameroon, Tsch'a Bekom, Bamenda District, no date, coll. Glauming.

***Trioceros perreti* (Klaver & Böhme, 1992)**

MHNG 920.068-9 (male paratype + female paratype), MHNG 964.038 (female paratype), MHNG 965.054 (male paratype), MHNG 1010.052 (male holotype), MHNG 1010.053 (male paratype) Cameroon, Manengouba Mts., 1956, coll. J.-L. Perret; MHNG 1365.011 (male paratype), Cameroon, Manengouba Mts., Mwandong, 26.II.1972,

coll. J.L. Amiet; MHNG 1365.012-18 (5 male paratypes + 2 female paratypes), Cameroon, Manengouba Mts., III.1973, coll. J.L. Amiet; MNHN 2007.1455-57 (3 females), Cameroon, Manengouba Mts., around Mouame-na village, 9.796°E/4.984°N, altitude 4450 ft, 28.IV.2007, coll. I. Ineich & N. Lhermitte-Vallarino; MNHN 2007.1458-60 (2 males), Cameroon, Manengouba Mts., around Mouabi village, 5.0613°N/9.8155°E, altitude 5283 ft, 29.IV.2007, coll. I. Ineich & N. Lhermitte-Vallarino; MNHN 2007.1460 (male), Cameroon, Manengouba Mts., border of the road going to the lakes, 5.0512°N/9.8069°E, 28.IV.2007, coll. I. Ineich & N. Lhermitte-Vallarino; ZFMK 5802-3 (2 male paratypes), Cameroon, Manengouba Mts., Lake Manengouba, 20.XII.1966-5.I.1967, coll. M. Eisentraut; ZFMK 55599 (male), Cameroon, Manengouba, river east of Lake Manengouba, no date, F. Le Berre; ZFMK 58896-7 (2 males), Cameroon, Manengouba Mts., 1993, coll. E. Wallikewitz; ZFMK 59030 (male), Cameroon, Manengouba Mts., 1994, from pet trade; ZFMK 61836 (male), Cameroon, Manengouba area, no date, F. Le Berre; ZFMK 62571 (male), Cameroon, Manengouba area, no data, coll. unknown; ZFMK 66579 (female), Cameroon, Manengouba area, no date, from pet trade; ZFMK 66738, ZFMK 66740 (2 males), Cameroon, Manengouba area, 1998, from pet trade; ZFMK 69828, ZFMK 69830 (male + female), Cameroon, Bakossi Mts., 5.I.1998, coll. O. Euskirchen; ZFMK 69848-51 (male + 3 females), Cameroon, Bakossi Mts., 5.I.1998, coll. A. Schmitz.

***Trioceros wiedersheimi* (Nieden, 1910)**

MHNG 1544.1-2 (2 females), Cameroon, Mayo Darlé, 1941, coll. R. de Kalbermatten; MNHN 2005.2753 (female), Cameroon, Fongoi Village, Tchabal Mbabo, 12.053°E/7.230°N, altitude 1900 m, 12.I.2002, coll. Programme CamHerp; NMP6V 74112 (male), Cameroon, Tchabal Gangdaba, 7°44.678'N 12°42.741'E, 1560 m a.s.l., 26.X.2009, coll. V. Gvoždík; ZFMK 47941 (male), Nigeria, Gotel Mts. Gangirwal, app. 2400 m a.s.l., 15.II.1988, coll. G. Nikolaus; ZFMK 68943 (male), Cameroon, Tchabal Mbabo, southern slopes, XI.-5.XII.1998, coll. George & Johnson; ZFMK 75740-3 (3 males + female), Cameroon, Mayo Kelele, app. 1600 m a.s.l., 7.II.2000, coll. H.-W. Herrmann & A. Schmitz; ZFMK 75744-6 (male + 2 females), Cameroon, Tchabal Mbabo, 25.I.2001, coll. H.-W. Herrmann & A. Schmitz; ZFMK 78714 (male), Cameroon, Tchabal Mbabo, I.2001, coll. H.-W. Herrmann & A. Schmitz; ZMB 21857, ZMB 74806 (formerly part of ZMB 21857) (male + female), Cameroon, Banjo Gebirge, no date, coll. Riggerbach; ZMB 21861, ZMB 74805 (formerly part of ZMB 21861) (male + female), Cameroon, Banjo Gebirge, no date, Riggerbach; ZMB 21873 (female lectotype), Cameroon, Genderogebirge, 1500 m a.s.l., no date, coll. Riggerbach.

## Appendix II

**Table 1.** List of voucher specimens for each species included in the present study, with their respective localities, collection numbers and GenBank accession numbers (16S, 12S) [\*sequence from Pook & Wild 1997; not in GenBank; same species but different vouchers used for 16S and 12S] [\*\*sequence from Pook & Wild 1997, not in GenBank; same voucher used for both sequences].

Species	Locality	Collection number	Accession number
<i>Kinyongia tavetana</i>	South Pare, Kilimanjaro, Tanzania	MHNG 2612.58	AM422414 / AM422433
<i>Trioceros oweni</i> [E146.15]	Nkoelon, Campo region	ZFMK 87642	HQ337816 / HQ337864
<i>Trioceros camerunensis</i> [E130.1]	Njonji, Mt. Cameroon	MNHN 2007.0037	HQ337798 / HQ337846
<i>Trioceros cristatus</i> [E130.2]	Njonji, Mt. Cameroon	MNHN 2007.1447	HQ337799 / HQ337847
<i>Trioceros cristatus</i> [E130.3]	Njonji, Mt. Cameroon	MNHN 2007.1448	HQ337800 / HQ337848
<i>Trioceros cristatus</i> [E131.1]	Njonji, Mt. Cameroon	MNHN 2007.1449	HQ337801 / HQ337849
<i>Trioceros cristatus</i> [E146.13]	Amebishu, Mamfe region	ZFMK 87646	HQ337802 / HQ337850
<i>Trioceros cristatus</i> [E150.7]	Amebishu, Mamfe region	ZFMK 87647	HQ337803 / HQ337851
<i>Trioceros cristatus</i> [E150.8]	Nkoelon, Campo region	ZFMK 87649	HQ337804 / HQ337852
<i>Trioceros cristatus</i> [E180.2]	Mofako Balue, Rumpi Hills	ZFMK 89455	HQ337805 / HQ337853
<i>Trioceros cristatus</i> [E180.7]	Big Massaka, Rumpi Hills	MNHG 2716.39	HQ337806 / HQ337854
<i>Trioceros montium</i> [E130.4]	Mt. Cameroon	MNHN 2007.1429	HQ337807 / HQ337855
<i>Trioceros montium</i> [E130.5]	Mt. Kupe	MNHN 2007.1445	HQ337808 / HQ337856
<i>Trioceros montium</i> [E131.2]	Mt. Cameroon	MNHN 2007.1430	HQ337809 / HQ337857
<i>Trioceros montium</i> [E131.3]	Mt. Kupe	MNHN 2007.1446	HQ337810 / HQ337858
<i>Trioceros montium</i> [E179.18]	Mofako Balue, Rumpi Hills	MNHG 2716.47	HQ337811 / HQ337859
<i>Trioceros montium</i> [E180.15]	Nyasoso, Mt. Kupe	MNHG 2716.41	HQ337812 / HQ337860
<i>Trioceros montium</i> [E188.18]	Edib Hills, Bakossi Mts.	NMP6V 74130/2	HQ337813 / HQ337861
<i>Trioceros montium</i> [E188.19]	Edib Hills, Bakossi Mts.	NMP6V 74130/1	HQ337814 / HQ337862
<i>Trioceros montium</i> [E188.20]	Edib Hills, Bakossi Mts.	NMP6V 74130/3	HQ337815 / HQ337863
<i>Trioceros perreti</i> [E130.11]	Mts. Manengouba	MNHN 2007.1458	HQ337828 / HQ337876
<i>Trioceros perreti</i> [E130.12]	Mts. Manengouba	MNHN 2007.1459	HQ337829 / HQ337877
<i>Trioceros perreti</i> [E131.6]	Mts. Manengouba	MNHN 2007.1460	HQ337830 / HQ337875
<i>Trioceros pfefferi</i>	Afua Ijim Forest, 10,4°E/6,15°N	MNHN 2007.1499	HQ337817 / —*
<i>Trioceros quadricornis eisentrauti</i>	Rumpi Hills	voucher not collected	HQ337820 / —**
<i>Trioceros quadricornis eisentrauti</i> [E178.10]	Mt. Rata, Rumpi Hills	ZFMK 89466	HQ337818 / HQ337866
<i>Trioceros quadricornis eisentrauti</i> [E178.11]	Mt. Rata, Rumpi Hills	MNHG 2716.40	HQ337819 / HQ337867
<i>Trioceros quadricornis gracilior</i> [E130.7]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1426	HQ337821 / HQ337868
<i>Trioceros quadricornis gracilior</i> [E130.8]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1423	HQ337822 / HQ337869
<i>Trioceros quadricornis gracilior</i> [E131.4]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1424	HQ337823 / HQ337870
<i>Trioceros quadricornis quadricornis</i> [E130.9]	Mts. Manengouba	MNHN 2007.1470	HQ337824 / HQ337871
<i>Trioceros quadricornis quadricornis</i> [E130.10]	Mts. Manengouba	MNHN 2007.1466	HQ337825 / HQ337872
<i>Trioceros quadricornis quadricornis</i> [E131.5]	Mts. Manengouba	MNHN 2007.1469	HQ337826 / HQ337873
<i>Trioceros quadricornis quadricornis</i> [E131.8]	Mts. Manengouba	MNHN 2007.1468	HQ337827 / HQ337874
<i>Trioceros serratus</i> [E130.15]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1463	HQ337831 / HQ337878
<i>Trioceros serratus</i> [E130.16]	Lake Oku, Mt. Oku, Bamenda Highlands	MNHN 2007.1465	HQ337832 / HQ337879
<i>Trioceros serratus</i> [E130.17] (NEOTYPE)	Belo, Mt. Oku	MNHN 2007.1494	HQ337833 / HQ337880
<i>Trioceros serratus</i> [E131.7]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1464	HQ337834 / HQ337881
<i>Trioceros serratus</i> [E131.16]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1461	HQ337835 / HQ337882
<i>Trioceros serratus</i> [E131.17]	Oku village, Mt. Oku, Bamenda Highlands	MNHN 2007.1462	HQ337836 / HQ337883
<i>Trioceros serratus</i> [E178.2]	Mt. Mbam	voucher not collected	HQ337837 / HQ337884
<i>Trioceros serratus</i> [E178.3]	Mt. Mbam	voucher not collected	HQ337838 / HQ337885
<i>Trioceros serratus</i> [E178.4]	Mt. Mbam	voucher not collected	HQ337839 / HQ337886
<i>Trioceros serratus</i> [E178.5]	Mt. Mbam	voucher not collected	HQ337840 / HQ337887
<i>Trioceros serratus</i> [E188.16]	Big Babanki, Bamenda Highlands	NMP6V 74104	HQ337841 / HQ337888
<i>Trioceros serratus</i> [E189.8]	Big Babanki, Bamenda Highlands	voucher not collected	HQ337842 / HQ337889
<i>Trioceros wiedersheimi</i> [E91.6]	Tchabal Mbabo	ZFMK 75744	HQ337843 / HQ337890
<i>Trioceros wiedersheimi</i> [E178.1]	Tchabal Mbabo	voucher not collected	HQ337844 / HQ337891
<i>Trioceros wiedersheimi</i> [E188.13]	Tchabal Gangdaba	NMP6V 74112	HQ337845 / HQ337892



Table 2. Uncorrected *p*-distances between Cameroonian *Trioceros* taxa based on 960 bp of the 16S + 12S rRNA gene fragments.

	1	2	3	4	5	6	7	8	9	10	11	12
1 <i>Kinyongia tavetana</i> AM422414/AM422433	–											
2 <i>oweni</i> Nkoelon, Campo region [E146.15]	0.1221	–										
3 <i>camerunensis</i> Mt. Cameroon [E130.1]	0.1230	0.0986	–									
4 <i>cristatus</i> Big Massaka, Rumpi Hills [E180.7]	0.1138	0.0868	0.0381	–								
5 <i>cristatus</i> Nkoelon, Campo region [E150.8]	0.1109	0.0868	0.0386	0.0086	–							
6 <i>cristatus</i> Amebishu, Mamfe region [E146.13]	0.1083	0.0857	0.0402	0.0095	0.0075	–						
7 <i>cristatus</i> Amebishu, Mamfe region [E150.7]	0.1095	0.0868	0.0412	0.0106	0.0086	0.0011	–					
8 <i>cristatus</i> Njonji, Mt. Cameroon [E130.2]	0.1151	0.0890	0.0396	0.0011	0.0096	0.0107	0.0118	–				
9 <i>cristatus</i> Njonji, Mt. Cameroon [E130.3]	0.1162	0.0901	0.0407	0.0021	0.0107	0.0118	0.0128	0.0011	–			
10 <i>cristatus</i> Njonji, Mt. Cameroon [E131.1]	0.1150	0.0879	0.0391	0.0011	0.0096	0.0105	0.0116	0.0000	0.0011	–		
11 <i>cristatus</i> Mofako Balue, Rumpi Hills [E180.2]	0.1138	0.0868	0.0381	0.0000	0.0086	0.0095	0.0106	0.0011	0.0021	0.0011	–	
12 <i>montium</i> Edib Hills, Bakossi Mts. [E188.20]	0.1159	0.0958	0.0343	0.0365	0.0326	0.0365	0.0376	0.0380	0.0391	0.0375	0.0365	–
13 <i>montium</i> Edib Hills, Bakossi Mts. [E188.18]	0.1152	0.0943	0.0338	0.0360	0.0321	0.0360	0.0370	0.0375	0.0385	0.0370	0.0360	0.0000
14 <i>montium</i> Edib Hills, Bakossi Mts. [E188.19]	0.1152	0.0943	0.0338	0.0360	0.0321	0.0360	0.0370	0.0375	0.0385	0.0370	0.0360	0.0000
15 <i>montium</i> Mt. Kupe [E130.5]	0.1153	0.0944	0.0374	0.0386	0.0332	0.0375	0.0385	0.0396	0.0407	0.0396	0.0386	0.0032
16 <i>montium</i> Mt. Kupe [E131.3]	0.1153	0.0944	0.0374	0.0386	0.0332	0.0375	0.0385	0.0396	0.0407	0.0396	0.0386	0.0032
17 <i>montium</i> Nyasoso, Mt. Kupe [E180.15]	0.1152	0.0943	0.0338	0.0360	0.0321	0.0360	0.0370	0.0375	0.0385	0.0370	0.0360	0.0000
18 <i>montium</i> Mt. Cameroon [E130.4]	0.1153	0.0964	0.0381	0.0392	0.0364	0.0402	0.0413	0.0407	0.0418	0.0402	0.0392	0.0064
19 <i>montium</i> Mt. Cameroon [E131.2]	0.1153	0.0964	0.0381	0.0392	0.0364	0.0402	0.0413	0.0407	0.0418	0.0402	0.0392	0.0064
20 <i>montium</i> Mofako Balue, Rumpi Hills [E179.18]	0.1141	0.0923	0.0349	0.0360	0.0311	0.0349	0.0360	0.0375	0.0385	0.0370	0.0360	0.0011
21 <i>perreti</i> Mts. Manengouba [E131.6]	0.1194	0.0943	0.0623	0.0528	0.0525	0.0560	0.0571	0.0545	0.0556	0.0539	0.0528	0.0591
22 <i>perreti</i> Mts. Manengouba [E130.11]	0.1227	0.0953	0.0612	0.0517	0.0514	0.0549	0.0560	0.0534	0.0545	0.0528	0.0517	0.0580
23 <i>perreti</i> Mts. Manengouba [E130.12]	0.1227	0.0953	0.0612	0.0517	0.0514	0.0549	0.0560	0.0534	0.0545	0.0528	0.0517	0.0580
24 <i>pfefferi</i>	0.1099	0.0934	0.0627	0.0603	0.0563	0.0588	0.0575	0.0616	0.0629	0.0616	0.0603	0.0538
25 <i>quadricornis eisentrauti</i> Rumpi Hills	0.1058	0.0966	0.0690	0.0639	0.0614	0.0612	0.0626	0.0652	0.0665	0.0652	0.0639	0.0611
26 <i>quadricornis eisentrauti</i> Mt. Rata, Rumpi Hills [E178.10]	0.1118	0.0948	0.0638	0.0605	0.0591	0.0606	0.0617	0.0621	0.0632	0.0616	0.0605	0.0551
27 <i>quadricornis eisentrauti</i> Mt. Rata, Rumpi Hills [E178.11]	0.1124	0.0957	0.0644	0.0611	0.0598	0.0611	0.0623	0.0629	0.0640	0.0622	0.0611	0.0556
28 <i>quadricornis gracilior</i> Mt. Oku [E130.7]	0.1117	0.0911	0.0603	0.0539	0.0525	0.0539	0.0550	0.0556	0.0567	0.0550	0.0539	0.0526
29 <i>quadricornis gracilior</i> Mt. Oku [E130.8]	0.1117	0.0911	0.0603	0.0539	0.0525	0.0539	0.0550	0.0556	0.0567	0.0550	0.0539	0.0526
30 <i>quadricornis gracilior</i> Oku village [E131.4]	0.1118	0.0922	0.0610	0.0545	0.0525	0.0545	0.0557	0.0556	0.0567	0.0556	0.0545	0.0532
31 <i>quadricornis quadricornis</i> Mts. Manengouba [E130.10]	0.1105	0.0933	0.0624	0.0560	0.0547	0.0560	0.0571	0.0577	0.0588	0.0571	0.0560	0.0548
32 <i>quadricornis quadricornis</i> Mts. Manengouba [E130.9]	0.1105	0.0933	0.0624	0.0560	0.0547	0.0560	0.0571	0.0577	0.0588	0.0571	0.0560	0.0548
33 <i>quadricornis quadricornis</i> Mts. Manengouba [E131.5]	0.1105	0.0933	0.0624	0.0560	0.0547	0.0560	0.0571	0.0577	0.0588	0.0571	0.0560	0.0548
34 <i>quadricornis quadricornis</i> Mts. Manengouba [E131.8]	0.1108	0.0944	0.0632	0.0567	0.0546	0.0567	0.0579	0.0578	0.0589	0.0578	0.0567	0.0554
35 <i>serratus</i> Belo, Mt. Oku [E130.17]	0.1174	0.1008	0.0651	0.0609	0.0601	0.0619	0.0620	0.0621	0.0632	0.0620	0.0609	0.0641
36 <i>serratus</i> Big Babanki, Bamenda Highlands [E188.16]	0.1174	0.0998	0.0646	0.0603	0.0601	0.0614	0.0615	0.0621	0.0632	0.0614	0.0603	0.0635
37 <i>serratus</i> Big Babanki, Bamenda Highlands [E189.8]	0.1180	0.1014	0.0654	0.0611	0.0609	0.0622	0.0623	0.0629	0.0640	0.0622	0.0611	0.0634
38 <i>serratus</i> Mt. Mbam [E178.2]	0.1163	0.1000	0.0664	0.0621	0.0612	0.0632	0.0633	0.0632	0.0643	0.0632	0.0621	0.0653
39 <i>serratus</i> Mt. Mbam [E178.3]	0.1165	0.0990	0.0654	0.0611	0.0602	0.0622	0.0622	0.0622	0.0633	0.0622	0.0611	0.0643
40 <i>serratus</i> Mt. Mbam [E178.4]	0.1163	0.0999	0.0664	0.0621	0.0612	0.0632	0.0632	0.0632	0.0643	0.0632	0.0621	0.0653
41 <i>serratus</i> Mt. Mbam [E178.5]	0.1151	0.0977	0.0646	0.0603	0.0601	0.0614	0.0615	0.0621	0.0632	0.0614	0.0603	0.0635
42 <i>serratus</i> Mt. Oku [E130.15]	0.1186	0.1022	0.0664	0.0621	0.0613	0.0632	0.0633	0.0632	0.0643	0.0632	0.0621	0.0654
43 <i>serratus</i> Lake Oku [E130.16]	0.1186	0.1021	0.0663	0.0621	0.0612	0.0632	0.0632	0.0632	0.0643	0.0632	0.0621	0.0653
44 <i>serratus</i> Oku village [E131.16]	0.1175	0.0998	0.0646	0.0604	0.0601	0.0614	0.0626	0.0622	0.0633	0.0615	0.0604	0.0636
45 <i>serratus</i> Oku village [E131.17]	0.1185	0.1009	0.0656	0.0614	0.0612	0.0624	0.0625	0.0632	0.0643	0.0625	0.0614	0.0646
46 <i>serratus</i> Oku village [E131.7]	0.1090	0.0988	0.0680	0.0645	0.0636	0.0633	0.0634	0.0656	0.0667	0.0656	0.0645	0.0670
47 <i>wiedersheimi</i> Tchabal Mbabo [E91.6]	0.1147	0.0923	0.0635	0.0520	0.0529	0.0533	0.0534	0.0538	0.0550	0.0531	0.0520	0.0590
48 <i>wiedersheimi</i> Tchabal Mbabo [E178.1]	0.1163	0.0900	0.0620	0.0508	0.0494	0.0498	0.0498	0.0526	0.0537	0.0519	0.0508	0.0565
49 <i>wiedersheimi</i> Tchabal Gangdaba [E188.13]	0.1146	0.0903	0.0637	0.0519	0.0527	0.0530	0.0541	0.0536	0.0547	0.0530	0.0519	0.0592

Table 2. Continued.

	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
13	–																		
14	0.0000	–																	
15	0.0032	0.0032	–																
16	0.0032	0.0032	0.0000	–															
17	0.0000	0.0000	0.0032	0.0032	–														
18	0.0063	0.0063	0.0075	0.0075	0.0063	–													
19	0.0063	0.0063	0.0075	0.0075	0.0063	0.0000	–												
20	0.0011	0.0011	0.0021	0.0021	0.0011	0.0053	0.0053	–											
21	0.0582	0.0582	0.0578	0.0578	0.0582	0.0603	0.0603	0.0571	–										
22	0.0571	0.0571	0.0567	0.0567	0.0571	0.0592	0.0592	0.0560	0.0032	–									
23	0.0571	0.0571	0.0567	0.0567	0.0571	0.0592	0.0592	0.0560	0.0032	0.0000	–								
24	0.0535	0.0535	0.0521	0.0521	0.0535	0.0574	0.0574	0.0510	0.0365	0.0378	0.0378	–							
25	0.0599	0.0599	0.0587	0.0587	0.0599	0.0613	0.0613	0.0575	0.0370	0.0382	0.0382	0.0392	–						
26	0.0542	0.0542	0.0536	0.0536	0.0542	0.0563	0.0563	0.0522	0.0403	0.0435	0.0435	0.0368	0.0026	–					
27	0.0547	0.0547	0.0542	0.0542	0.0547	0.0568	0.0568	0.0526	0.0407	0.0439	0.0439	0.0369	0.0027	0.0000	–				
28	0.0518	0.0518	0.0513	0.0513	0.0518	0.0539	0.0539	0.0497	0.0433	0.0443	0.0443	0.0366	0.0102	0.0106	0.0107	–			
29	0.0518	0.0518	0.0513	0.0513	0.0518	0.0539	0.0539	0.0497	0.0433	0.0443	0.0443	0.0366	0.0102	0.0106	0.0107	0.0000	–		
30	0.0524	0.0524	0.0513	0.0513	0.0524	0.0545	0.0545	0.0503	0.0438	0.0448	0.0448	0.0366	0.0103	0.0107	0.0108	0.0000	0.0000	–	
31	0.0539	0.0539	0.0535	0.0535	0.0539	0.0560	0.0560	0.0518	0.0422	0.0432	0.0432	0.0367	0.0051	0.0064	0.0064	0.0063	0.0063	0.0064	–
32	0.0539	0.0539	0.0535	0.0535	0.0539	0.0560	0.0560	0.0518	0.0422	0.0432	0.0432	0.0367	0.0051	0.0064	0.0064	0.0063	0.0063	0.0064	0.0000
33	0.0539	0.0539	0.0535	0.0535	0.0539	0.0560	0.0560	0.0518	0.0422	0.0432	0.0432	0.0367	0.0051	0.0064	0.0064	0.0063	0.0063	0.0064	0.0000
34	0.0546	0.0546	0.0535	0.0535	0.0546	0.0567	0.0567	0.0525	0.0427	0.0438	0.0438	0.0367	0.0051	0.0064	0.0065	0.0064	0.0064	0.0064	0.0000
35	0.0630	0.0630	0.0622	0.0622	0.0630	0.0652	0.0652	0.0620	0.0458	0.0447	0.0447	0.0434	0.0435	0.0480	0.0487	0.0426	0.0426	0.0427	0.0437
36	0.0625	0.0625	0.0622	0.0622	0.0625	0.0646	0.0646	0.0614	0.0454	0.0444	0.0444	0.0434	0.0435	0.0478	0.0483	0.0423	0.0423	0.0428	0.0433
37	0.0634	0.0634	0.0631	0.0631	0.0634	0.0655	0.0655	0.0623	0.0461	0.0451	0.0451	0.0437	0.0442	0.0484	0.0489	0.0428	0.0428	0.0433	0.0439
38	0.0643	0.0643	0.0632	0.0632	0.0643	0.0664	0.0664	0.0632	0.0459	0.0448	0.0448	0.0434	0.0435	0.0471	0.0477	0.0416	0.0416	0.0417	0.0427
39	0.0633	0.0633	0.0622	0.0622	0.0633	0.0654	0.0654	0.0622	0.0449	0.0438	0.0438	0.0434	0.0435	0.0460	0.0467	0.0406	0.0406	0.0407	0.0417
40	0.0643	0.0643	0.0632	0.0632	0.0643	0.0664	0.0664	0.0632	0.0459	0.0448	0.0448	0.0434	0.0435	0.0471	0.0477	0.0416	0.0416	0.0417	0.0427
41	0.0625	0.0625	0.0622	0.0622	0.0625	0.0646	0.0646	0.0614	0.0444	0.0433	0.0433	0.0447	0.0448	0.0478	0.0482	0.0423	0.0423	0.0428	0.0433
42	0.0643	0.0643	0.0633	0.0633	0.0643	0.0665	0.0665	0.0633	0.0470	0.0460	0.0460	0.0447	0.0447	0.0493	0.0500	0.0438	0.0438	0.0439	0.0449
43	0.0643	0.0643	0.0632	0.0632	0.0643	0.0664	0.0664	0.0632	0.0470	0.0459	0.0459	0.0447	0.0447	0.0492	0.0499	0.0438	0.0438	0.0438	0.0449
44	0.0626	0.0626	0.0623	0.0623	0.0626	0.0647	0.0647	0.0615	0.0455	0.0444	0.0444	0.0446	0.0434	0.0479	0.0483	0.0423	0.0423	0.0428	0.0434
45	0.0636	0.0636	0.0633	0.0633	0.0636	0.0657	0.0657	0.0625	0.0465	0.0454	0.0454	0.0447	0.0447	0.0488	0.0493	0.0433	0.0433	0.0439	0.0444
46	0.0658	0.0658	0.0648	0.0648	0.0658	0.0669	0.0669	0.0647	0.0486	0.0475	0.0475	0.0447	0.0447	0.0475	0.0483	0.0419	0.0419	0.0419	0.0429
47	0.0591	0.0591	0.0587	0.0587	0.0591	0.0612	0.0612	0.0568	0.0374	0.0363	0.0363	0.0337	0.0318	0.0342	0.0345	0.0329	0.0329	0.0333	0.0329
48	0.0565	0.0565	0.0562	0.0562	0.0565	0.0609	0.0609	0.0543	0.0388	0.0377	0.0377	0.0340	0.0321	0.0345	0.0348	0.0333	0.0333	0.0337	0.0332
49	0.0583	0.0583	0.0580	0.0580	0.0583	0.0604	0.0604	0.0562	0.0413	0.0403	0.0403	0.0389	0.0341	0.0352	0.0354	0.0350	0.0350	0.0354	0.0360
	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	
32	–																		
33	0.0000	–																	
34	0.0000	0.0000	–																
35	0.0437	0.0437	0.0438	–															
36	0.0433	0.0433	0.0439	0.0000	–														
37	0.0439	0.0439	0.0445	0.0000	0.0000	–													
38	0.0427	0.0427	0.0428	0.0011	0.0011	0.0011	–												
39	0.0417	0.0417	0.0417	0.0011	0.0011	0.0011	0.0000	–											
40	0.0427	0.0427	0.0428	0.0011	0.0011	0.0011	0.0000	0.0000	–										
41	0.0433	0.0433	0.0439	0.0021	0.0021	0.0021	0.0011	0.0011	0.0011	–									
42	0.0449	0.0449	0.0450	0.0011	0.0011	0.0011	0.0021	0.0021	0.0021	0.0032	–								
43	0.0449	0.0449	0.0449	0.0011	0.0011	0.0011	0.0021	0.0021	0.0021	0.0032	0.0000	–							
44	0.0434	0.0434	0.0439	0.0021	0.0021	0.0022	0.0032	0.0032	0.0032	0.0042	0.0011	0.0011	–						
45	0.0444	0.0444	0.0449	0.0011	0.0011	0.0011	0.0021	0.0022	0.0021	0.0032	0.0000	0.0000	0.0011	–					
46	0.0429	0.0429	0.0430	0.0011	0.0011	0.0012	0.0023	0.0023	0.0023	0.0034	0.0000	0.0000	0.0011	0.0000	–				
47	0.0329	0.0329	0.0334	0.0344	0.0341	0.0340	0.0333	0.0322	0.0333	0.0341	0.0357	0.0356	0.0352	0.0352	0.0378	–			
48	0.0332	0.0332	0.0337	0.0369	0.0365	0.0365	0.0359	0.0348	0.0359	0.0365	0.0382	0.0381	0.0377	0.0376	0.0403	0.0045	–		
49	0.0360	0.0360	0.0365	0.0375	0.0371	0.0377	0.0365	0.0355	0.0365	0.0371	0.0387	0.0386	0.0372	0.0382	0.0408	0.0068	0.0066	–	

**Table 3.** Summary of morphological measures (mm) of adult male and female *Trioceros perreti*, *T. wiedersheimi* and *T. serratus*. Given are sample size (N), minimum (min), maximum (max), mean values (mean) and standard deviation (s.dev.) GC = number of scales forming gular crest, BL = body length from tip of snout to cloaca, TL = tail length from cloaca to tip of tail, ED = vertical eye diameter, StHt = distance snout tip to tip of helmet, HW = head width, MG = mouth gap, MGHT = distance mouth gap to tip of helmet, TiL = tibia length, FoL = fore arm length, GL = length of gular crest, SHE = number of scale between eye and end of head, FSM = flank scales at midbody, TL/BL = tail length / body length ratio, TiL/BL = tibia length / body length ratio, FoL/BL forearm length / body length ratio, MG/StHt = mouth gap / snout tip to tip of helmet ratio, HW/StHt = head width / snout tip to tip of helmet ratio, ED/MG = eye diameter / mouth gap ratio, MG/MGHT = mouth gap / mouth gap to tip of helmet ratio.

	GC	BL	TL	ED	StHt	HW	MG	MGHT	TiL	FoL	GL	SHE	FSM	TL/BL	TiL/BL	FoL/BL	MG/StHt	HW/StHt	ED/MG	ED/HW	ED/MG	G/MGHT	
<b><i>Trioceros perreti</i> (males)</b>																							
N	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
min	11	63.0	53.0	6.1	21.0	6.5	10.3	14.4	10.1	11.1	0.5	9	65	0.72	0.14	0.15	0.47	0.28	0.54	0.94	0.54	0.54	0.68
max	37	81.0	74.0	8.0	26.0	9.7	13.6	17.7	14.2	15.3	1.3	15	93	1.04	0.18	0.20	0.55	0.38	0.63	1.25	0.63	0.63	0.82
mean	21.4	74.2	64.6	6.9	23.1	7.6	11.8	16.0	12.0	12.8	0.9	11	75	0.87	0.16	0.17	0.51	0.33	0.58	1.12	0.58	0.58	0.73
s.dev.	6	4.4	5.9	0.5	1.4	0.7	0.8	1.0	0.9	1.0	0.2	1.7	6.6	0.08	0.01	0.01	0.02	0.02	0.02	0.07	0.02	0.02	0.04
<b><i>Trioceros wiedersheimi</i> (males)</b>																							
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
min	14	61.0	60.5	5.8	19.7	6.4	9.9	13.4	10.6	11.0	1.4	5	57	0.89	0.15	0.16	0.47	0.32	0.57	1.03	0.57	0.57	0.69
max	23	100.5	107.5	8.2	26.3	9.1	13.1	18.1	16.7	17.6	2.2	8	64	1.10	0.18	0.19	0.53	0.36	0.64	1.23	0.64	0.64	0.83
mean	18.2	80.4	82.6	7.0	22.8	7.9	11.5	15.7	13.5	14.3	1.8	7	61	1.02	0.17	0.18	0.50	0.35	0.61	1.14	0.61	0.61	0.74
s.dev.	3	13.4	17.9	0.9	2.2	0.8	1.3	1.6	2.0	2.3	0.3	1.2	2.1	0.07	0.01	0.01	0.02	0.02	0.02	0.07	0.02	0.02	0.04
<b><i>Trioceros serratus</i> (males)</b>																							
N	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27
min	15	52.0	46.5	5.4	17.0	6.0	8.3	11.6	8.2	8.4	0.8	6	56	0.83	0.15	0.15	0.47	0.30	0.55	1.04	0.55	0.55	0.68
max	29	88.0	91.0	8.1	25.2	10.3	13.3	17	14.4	15.0	2.7	10	76	1.03	0.17	0.18	0.55	0.43	0.65	1.34	0.65	0.65	0.86
mean	21.9	74.9	69.0	6.7	22.3	8.0	11.5	15	12.1	12.6	1.6	8	65	0.92	0.16	0.17	0.51	0.36	0.59	1.19	0.59	0.59	0.76
s.dev.	4	8.5	9.4	0.7	2.2	1.0	1.3	1	1.4	1.5	0.4	1.2	5.4	0.06	0.01	0.01	0.02	0.03	0.02	0.06	0.02	0.02	0.04
<b><i>Trioceros perreti</i> (females)</b>																							
N	12	12	10	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
min	12	70.0	54.0	6.2	21.7	6.7	11.1	14.4	11.5	11.6	0.6	9	67	0.75	0.15	0.15	0.49	0.28	0.53	1.00	0.53	0.53	0.72
max	30	95.0	67.0	7.5	27.2	8.5	13.5	18.2	14.6	15.1	1.0	12	83	0.90	0.18	0.19	0.54	0.34	0.58	1.22	0.58	0.58	0.82
mean	20.5	78.3	62.0	6.7	23.4	7.5	12.1	15.9	12.8	13.3	0.8	11	73	0.81	0.16	0.17	0.51	0.32	0.56	1.18	0.56	0.56	0.76
s.dev.	7	7.4	3.6	0.4	1.4	0.5	0.7	1.1	0.9	1.1	0.1	1.0	5.2	0.05	0.01	0.01	0.02	0.02	0.01	0.06	0.01	0.01	0.03
<b><i>Trioceros wiedersheimi</i> (females)</b>																							
N	9	9	8	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
min	15	68.0	52.0	6.3	20.5	6.6	10.4	13.7	11.6	12.0	1.0	5	57	0.76	0.16	0.16	0.48	0.30	0.55	0.97	0.55	0.55	0.71
max	23	87.0	86.0	7.7	25.4	8.4	13.3	16.3	13.9	15.0	2.5	9	68	1.00	0.17	0.18	0.53	0.36	0.61	1.21	0.61	0.61	0.84
mean	19.4	78.9	67.0	6.9	22.9	7.4	11.8	15.2	12.9	13.5	1.5	7	63	0.86	0.16	0.17	0.52	0.33	0.58	1.09	0.58	0.58	0.78
s.dev.	3	6.7	9.8	0.5	1.7	0.5	1.0	0.9	0.8	1.1	0.5	1.1	3.4	0.08	0.01	0.01	0.02	0.02	0.02	0.08	0.02	0.02	0.05
<b><i>Trioceros serratus</i> (females)</b>																							
N	17	17	15	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17
min	19	55.0	45.0	5.5	18.1	5.5	8.8	12.0	8.5	9.0	0.6	6	60	0.63	0.15	0.14	0.47	0.29	0.52	1.01	0.52	0.52	0.70
max	31	92.0	70.0	7.5	24.8	9.3	13.4	16.8	14.5	14.9	1.9	11	76	0.86	0.18	0.18	0.58	0.38	0.63	1.27	0.63	0.63	0.87
mean	23.1	74.6	57.4	6.5	21.7	7.3	11.4	14.4	11.9	12.3	1.3	8	67	0.77	0.16	0.16	0.52	0.34	0.57	1.12	0.57	0.57	0.79
s.dev.	3	10.3	7.2	0.7	2.1	1.1	1.5	1.4	1.7	1.8	0.4	1.2	4.4	0.06	0.01	0.01	0.03	0.03	0.03	0.08	0.03	0.03	0.05